

Sown wildflower strips for insect conservation: a review

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Abstract. 1. Sown wildflower strips are increasingly being established in European countries within agri-environmental schemes to enhance biodiversity, especially in intensively used agricultural areas.

2. The regulations vary between countries regarding the seed mixture, intensity of management and period of time over which subsidies are given. Insects in particular are intended to benefit from these schemes.

3. This review treats studies of insect diversity and abundance in sown wildflower strips. Schemes on wildflower strips in several countries in Central and Northern Europe are compared.

4. In a significant majority of studies, sown wildflower strips support higher insect abundances and diversity than cropped habitats. In general, numbers and diversity also tend to be higher than in other margin types such as sown grass margins and natural regeneration, but pollen- and nectar-rich flower mixtures may outperform them.

5. Common species are the main beneficiaries of the establishment of wildflower strips, although some studies point out the presence of rare or declining insect species.

6. Insect groups respond differently to particular characteristics of the strips. Flower abundance, seed mixture, vegetation structure, management, age and landscape have been identified as factors influencing insect abundance and diversity.

7. Future work should address under-represented comparisons, such as with pollen- and nectar-rich seed mixes, and neglected groups, in particular parasitoids. Nevertheless, sown wildflower strips can already be seen as a beneficial measure to enhance insect diversity. This is especially the case, where schemes for sown strips vary within a region to favour different species groups.

Key words. Agri-environmental scheme, field margin, pollen–nectar flower mixture, set aside, wildflower areas.

Introduction

The intensification of agriculture over recent decades has caused a severe decline of biodiversity in agricultural landscapes throughout Europe. Habitat destruction, habitat deterioration

by intensification and the consequential change of landscape patterns has caused the loss or decline of many species (Kruess & Tscharntke, 1994; Stoate *et al.*, 2001; Jongman, 2002). Agricultural policies in Europe have therefore been adopted in an attempt to mitigate the impact of agriculture on biodiversity with the help of cross compliance rules and agri-environmental schemes (AES). The benefits of these schemes for biodiversity have recently been disputed, especially with regard to their very high costs (Kleijn & Sutherland, 2003; Berendse *et al.*, 2004; Whitfield, 2006; Whittingham, 2007), but it has been argued that

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they have often been judged according to criteria, such as the conservation of rare species, for which they were not designed (Potts *et al.*, 2006). Both positive and zero effects of AES on certain aspects of biodiversity have been revealed by the increasing number of studies on this topic (e.g. Feehan *et al.*, 2005; Kleijn *et al.*, 2006; Albrecht *et al.*, 2007; Kohler *et al.*, 2007).

Sown wildflower strips have been introduced as agri-environmental measures in several European countries to enhance biodiversity. The strips are usually sown with seed mixtures of wild flowers on arable land along field boundaries. The width, the species mixtures and the management of the strips vary between countries according to the current regulations. Sometimes these seed mixtures are also used on set-aside land, to produce habitats known as 'wildflower areas'. The seed mixture contains either wildflower seeds alone or in combination with grass seeds. Additionally, there exist schemes with sown strips containing mostly legume species to benefit bees and bumblebees in particular (called pollen & nectar mixture), and sown grass margins containing only seed mixtures of grasses. There is no uniform term for sown wildflower strips or wildflower areas, and they are also known as (sown) wildflower margins, wildflower resource patches, flowering strips, flowering plant strips, (artificial) flower-rich margins or borders, sown weed strips, improved field margins, sown field margin strips, or wildlife seed mixture margins.

Sown wildflower strips are in several ways an atypical agri-environmental measure because these strips are not a semi-natural habitat that existed in agricultural landscapes in that form before the 1990s. Most AES are directed towards the management, restoration or re-creation of semi-natural habitats that occurred in the agricultural landscape of the particular country before post-war intensification. In that perspective, sown wildflower strips are, at least in Central and Northern Europe, a rather new landscape element. In some countries, for example the UK, hay meadows are used as a model for the creation of wildflower strips. Elsewhere, including Switzerland and Germany, certain types of wildflower strips are sown without grass seeds and therefore have a quite different species composition than meadows. In these cases, there are no 'traditional' examples for the creation and management of sown wildflower strips, so seed mixtures and management have to be designed to fulfil the intended biodiversity objectives.

Sown wildflower strips are often directed in particular towards insect conservation. Besides enhancing biodiversity in the agricultural landscape, there are two crucial aims concerning insects that are mentioned as reasons for establishing wildflower strips: favouring pollinators to ensure crop pollination and contributing to biological pest control by favouring predators. The importance of invertebrate conservation because of their significance for ecosystem services has recently been highlighted (Haslett, 2007). Other objectives are to increase plant diversity at field margins, to support birds by providing food resources in the form of seeds and invertebrates, and to enhance amenity by creating areas with attractive flowers (Scott, 1996; Marshall & Moonen, 2002; Jacot *et al.*, 2007).

Like many groups, insect populations have declined rapidly in agricultural landscapes in Europe. In the case of pollinators this has been shown to have a negative effect on agricultural pro-

duction of some crops, including field bean and oilseed rape (Aizen *et al.*, 2009). Bumblebees, for example, have decreased throughout Northern and Central Europe (Backman & Tiainen, 2002; Mand *et al.*, 2002; Carvell *et al.*, 2006a, 2007; Fitzpatrick *et al.*, 2007; Kosior *et al.*, 2007; Goulson *et al.*, 2008). The causes for the decline are seen in the loss of habitat and foraging opportunities. Perhaps one of the best-documented declines of insects is that of butterflies and moths (Maes & Van Dyck, 2001; Conrad *et al.*, 2006; van Swaay *et al.*, 2006; Wenzel *et al.*, 2006; Kuussaari *et al.*, 2007; Polus *et al.*, 2007; Nilsson *et al.*, 2008), with habitat loss and fragmentation – especially of semi-natural meadows and pastures – given as the main reasons. The picture is similar for other insect groups, for example beetles (Kotze & O'Hara, 2003), bugs (Frank & Künzle, 2006) and bees (Biesmeijer *et al.*, 2006; Kohler *et al.*, 2007), and the general homogenisation of the agricultural landscape is seen as one important factor driving these trends (Benton *et al.*, 2003; Tschardt *et al.*, 2005; Diekötter *et al.*, 2008).

Here, we provide an overview of studies on sown wildflower strips and their effect on insect abundance and diversity, to evaluate their value as an AES. We begin with a brief description of AES in several European countries to illustrate the variation in approaches to the design and management of wildflower strips. We then review published studies that compare insect abundance and diversity in sown wildflower strips and alternative field margin types on arable land, and finish by discussing the implications for the design of wildflower strips for insect conservation.

Materials and methods

A short overview of sown wildflower strips as AES in EU countries in Central and Northern Europe was used to compare the different designs and management strategies. The major sources of information were the 'Rural development programmes' for the years 2007–2013 of the EU member states. These programmes, which each EU member state is obliged to prepare and which have to be acknowledged by the EU commission, include a description of the regulations for all the AES. It was not possible to compare the programmes of all concerned EU member states because of language constraints (English versions were not always available) and lack of availability (no downloads available via internet and no reply on requests to send electronic files or a paper version).

To contrast insect abundance and diversity in wildflower strips in comparison with other habitat types, literature searches within the ISI Web of Science were carried out in June 2008 and throughout autumn 2008 with the following key words: wildflower strip or wild flower strip; sown strip; sown margin; wildflower margin or wild flower margin; wildflower mixture; wildflower area or wild flower area. From the resulting articles, a selection was made of those focusing on insect diversity in sown wildflower strips. By far the majority of articles were from Europe and overwhelmingly from the UK and Switzerland, which both have had schemes for a long period. It was therefore decided to restrict this review to Central and Northern Europe.

A simple meta-analysis was carried out on the collection of studies, using binomial sign tests to determine if a significant majority of studies showed a positive or negative effect of wildflower strips on abundance and on diversity in comparison with each alternative habitat type. Tests were two-tailed, and studies that reported no difference was treated conservatively by assigning a half count to positive and half to negative.

Results

Sown wildflower strips and areas as agri-environmental schemes in different European countries

There are several countries in which sown wildflower strips or areas are established by farmers within AES (Table 1). The UK has a long tradition of establishing these areas (Scott, 1996; Boatman *et al.*, 1999), and today farmers have several options for sowing margins on arable land or set aside (a short overview is given in Pywell *et al.*, 2007). There exist schemes for establishing and maintaining 2–6 m wide buffer strips sown with a grass mixture and strips sown with a pollen and nectar flower mixture (at least 6 m wide). Pollen and nectar seed mixtures can also be applied on set-aside land. Within supplementary schemes strips can be sown with a recommended seed mixture containing grass and wildflower species. There is also the option for allowing natural succession on field margins. Management regulations vary between the different schemes, but generally fertilisation is prohibited, herbicide application is – if not totally forbidden – limited to spot-treatment of certain weeds, and cutting is reduced to a maximum of once per year, sometimes less. Pollen & nectar strips/areas can be grazed in autumn and winter.

In Switzerland, sown wildflower strips and areas have also been established for over 10 years (Nentwig, 2000; Pfiffner & Wyss, 2004). The approach is unique in one aspect, as most farmers use the same seed mixture, which contains 24 wildflower species and no grass seeds. There is, however, also a seed mixture with 37 plant species available (Pfiffner & Wyss, 2004). Winter mowing is recommended to farmers on a voluntary basis, but in many cases there is no form of management besides spot-treatment of certain weed species. After a maximum of 7 years the strips have to be ploughed. At that time succession has often gone so far that the strips are dominated by grasses or one of the included species, *Dipsacus fullonum* (Dipsacales: Dipsacaceae), and invaded by bush and tree species. Nentwig (2000) gives a comprehensive overview of studies carried out in wildflower strips. A new form of sown wildflower strip, called ‘improved field margins’, was introduced in 2008 as an AES (Jacot *et al.*, 2007). The novel features are the seed mixture, which also contains grass species, and the management, as annual cutting is recommended (of half the margin). Swiss farmers are obliged to manage at least 7% of their used agricultural land as ‘ecological compensation areas’. Sown wildflower strips are one option, but 80% of ecological compensation areas are extensive grasslands, i.e. without manure treatment and cut after 15 June (Lips *et al.*, 2000; Aviron *et al.*, 2007a). Note that farmers receive greater subsidies, if their ecological compensation areas are part of a designed network.

Germany and Austria have more recently adopted sown wildflower strips and areas in their agri-environmental programmes. In both countries they were already established within contract farming (e.g. Kromp *et al.*, 2004). In Germany, the programmes vary between different states (*Länder*), but several have schemes for sown wildflower strips (established for one or several years). As in the UK, management is reduced to no or few cuttings, and fertiliser and herbicide application is forbidden. In some cases, cutting is only allowed to reduce weeds and permission has to be requested. Recommended seed mixtures may contain more than 30 plant species (as for example in Niedersachsen). In Austria, sown wildflower strips are one of the many environmental measures in the second Austrian development programme, and farmers are obliged to establish wildflower areas on at least 2% of their arable land. Cutting is recommended once a year.

In Sweden, there have been few programmes for enhancing biodiversity in field margins. The proportion of land used for arable is small and focus is more directed towards preservation of grasslands and wetlands. Nevertheless, since 2007 farmers in Sweden have the option to sow special seed mixtures on set-aside land within certain regional programmes. The possibility to sow wildflower strips within buffer strips along watercourses is under discussion. Finland also has – at least since 2007 – a scheme for so called ‘landscape set asides’ with the objective to contribute to landscape heterogeneity. On these set-asides flowering plants such as *Phacelia* (Solanales: Hydrophyllaceae), cornflowers or corn poppies are recommended. Sown wildflower strips along field margins exist only rarely in Scandinavian countries.

Insect abundance and diversity in sown wildflower strips compared with other habitats

Table 2 gives an overview of studies investigating insect abundance, diversity or other ecological aspects in wildflower strips. The most common approach was to compare wildflower strips with crop (or crop edges) and/or other margin types (Table 3). The comparisons involve grassland habitats (3 studies), sown grass strips (11 studies), margins with natural regeneration (7 studies) and strips sown with pollen- and nectar-rich plants (3 studies). Twelve studies investigated more than one type of wildflower strip, which could vary in seed mixture (eight studies) or age (six studies). Seed mixtures within the same study could differ as following:

- 1 wildflower species only and wildflowers combined with grasses, three studies,
- 2 wildflower species and grasses, but different types of grasses (fine leaved or tussock), three studies,
- 3 different proportions of different plant species, two studies.

Higher abundances of insects in wildflower strips or patches compared with crop edges or crop was shown in 14 out of 16 comparisons, and higher diversity in 11 out of 13 (a significant majority in both cases, Table 4). Two studies found higher abundances and diversity in cropped habitats. Sutherland *et al.* (2001) detected higher numbers and diversity of syrphids in a crop edge near to a disused railway line compared with

Table 1. Selection of countries that have schemes for sown wildflower strips, wildflower areas or set aside sown with flower mixtures in their 'Rural development programme, 2007–2013'.

State	Sown wildflower strips	Wild flower areas (sometimes as set aside)	Term	Seed mixtures	Size	Management
Austria	x	x	Flowering strips (Blühstreifen) Flowering areas (Blühflächen; Biodiversitätsflächen) Landscape set aside	At least two flowering species, for example clover, <i>Phacelia</i> , or sunflower. Can additionally contain grasses	Strips 2.5–12 m wide	Cutting after 1 August, once per year
Finland		x		For example <i>Phacelia</i> , cornflowers, poppies		
Germany*, Niedersachsen	x	x	Flowering strips (Blühstreifen) 'Colourful fallow' (Buntbrache)	30 species recommended including legumes, the mixture must contain several of these species and not more than 10% legumes	3–24 m wide	Cutting if necessary, but not between 1 April and 15 July
UK	x	x	Sown wildflower strips/pollen & nectar flower mixture	Mixture of wildflowers and grasses or pollen & nectar flower mixture (legumes)	2–6 m wide, pollen strips at least 6 m wide	After the first year recommended to cut once per year after mid-September pollen and nectar strips can be grazed in winter
Switzerland	x	x	'Colourful fallow' (Buntbrache) Improved field margins (Säume) Biodiversity fallow (Mängfaldsträda or bioträda)	Usually 24–37 wildflower species, no grasses	Variable, often at least 3–4 m wide	Cutting once per year is recommended but often not carried out
Sweden†		x		Recommended species include clover, melilot, black medic, bird's-foot-trefoil, vetch and chicory	At least 10 m wide	Occasional cutting is recommended, but not allowed before August

*Each *Land* has its own Rural development programme, several Länder offer schemes for wildflower strips.

†Schemes on set aside sown with seed mixtures in several *län* (counties).

Table 2. Overview of studies of insect abundance and/or diversity in sown wildflower strips or patches published in English (several studies include further non-insect taxa).

Country	Taxon	Type of strip establishment*	Habitats investigated	Sampling methods	Results	Factors influencing abundance (A), species richness (R), diversity (D), and community composition (C)	Abundant/rare species	Reference
Germany	Arthropoda†	EP	1-year-old naturally developed strips (n = 4) 6-year-old naturally developed strips (n = 4) Phacelia strips (n = 4) Sown wildflower strips, 19 species (n = 4) Strips sown with winter wheat or oat (control) (n = 4) Field edge (n = 6)	Arthropod communities recorded on potted mugwort and red clover plants placed in the strips 1 year	No differences in species richness in the different strips, but three times higher species richness in strips than in field edges Higher predator-prey ratios in older strips compared to 1-year-old strips	Habitat type (R) Age (predator-prey ratio)	All arthropods were abundant and widespread species	Denys & Tschamtké (2002)
Netherlands	Apidae, Syrphidae	EP	Wildflower patches, 18 species (n = 5) Control (n = 50)	Sampling pollinators in wildflower patches and in controls at different distances 1 year	Species density and abundance of bees and hoverflies significantly enhanced in flower rich patches Insect diversity and abundance positively correlated with flower abundance	Habitat type (A, R) Flower abundance (A, D)		Kohler et al. (2008)
Sweden	Lepidoptera, Bombidae	EP	Sown wildflower strips, incl. grass species (n = 6) Strips sown with grasses (n = 14)	Butterfly and bumblebee observation along transects 1 year	Butterfly and bumblebee abundance and diversity higher in sown wildflower strips than in sown grass strips	Habitat type (A, D, C)	Almost all recorded species were common	Haaland & Gyllin (2010)
Switzerland	Overwintering Arthropoda‡	AES	Arable fields (n = 3) Ley (n = 1) Control, ploughed strip (n = 1) Sown wildflower strips, grass weed flower mix (n = 2) Sown wildflower strip, 25 species (n = 1) Permanent meadow strip (n = 1) Orchard (n = 1) Hedge (n = 1)	24 soil samples taken per habitat and in 6 pairs (arable, ley or control paired with adjacent field margin/habitat) 1 year	Much higher abundance and diversity of overwintering beetles in sown wildflower strips and other unploughed habitats than in controls	Habitat type (A, D)		Pfiffner & Luka (2000)
Switzerland	Meligethes pollen beetle (pest species on rape)	AES	Rape fields adjacent to wildflower strips (n = 11) Rape fields adjacent to extensively managed meadow (n = 15)	Measure of mortality, 3 and 30 m from the wildflower strip or meadow into the crop 4 years	Larval density higher at 3 m distance to strip or meadow than at 30 m distance Larval density decreased faster from edge into field when adjacent to meadow than with strip	Distance to strip (A) Year (mortality)		Büchi (2002)

Table 2. (Continued)

Country	Taxon	Type of strip establishment*	Habitats investigated	Sampling methods	Results	Factors influencing abundance (A), species richness (R), diversity (D), and community composition (C)	Abundant/rare species	Reference
Switzerland	Poecilus cupreus (Carabidae)	AES	1-4-year-old wildflower strips, 25 species (n = 16, four replicates for each year)	Number of ripe eggs and nutritional condition (weight/elytra length) of pitfall trapped individuals 1 year	Sig. fewer eggs in females within 1-year-old strips compared to 4-year-old strips Lower nutritional condition of individuals in 1-year-old strips compared to 2-4-year-old strips	Age (reproduction and nutritional condition)		Barone & Frank (2003)
Switzerland	Overwintering Staphylinidae, Carabidae	AES	1-3-year-old sown wildflower strips, 25 species (n = 12, four replicates for each year) Winter wheat fields (n = 4)	36 soil samples per site (on nine occasions) 1 year	Abundance and diversity of Staphylinidae similar between wheat fields and 1-year-old wildflower strips, then increased with age Abundance and diversity of Carabidae sig. higher in wildflower strips than in fields (highest in 2-3-year-old strips)	Habitat type (A, D) Age (A, D) Vegetation cover (C) Sand cover (C) Surrounding landscape (C)		Frank & Reichhart (2004)
Switzerland	Carabidae (five species)	AES	1-4-year-old sown wildflower areas, 25 species (n = 16, four replicates for each year)	Density and nutritional condition (weight/elytra length) of caught beetles 1 year	Abundance of one species increased with successional age of strips One species decreased with age Three species unaffected Nutritional condition of beetles increased with strip age	Age (A, nutritional condition)		Frank et al. (2007)
Switzerland	Heteroptera	AES	Sown wildflower areas (n = 5) Extensively used meadows (n = 5) Extensively grazed pastures (n = 5)	Bug collection using standardised sweep-netting 1 year	Highest abundance and diversity found in wildflower areas Diversity in wildflower areas and meadows sig. higher than in pastures	Habitat type (R, C) Vegetation structure (A, C) Flower abundance (C)	Several rare species occurred in wildflower areas	Zurbrugg & Frank (2006)
Switzerland	Heteroptera	AES	1-4-year-old sown wildflower strips (n = 16, four replicates for each year) Wheat fields (n = 4)	Bug collection using standardised sweep-netting 1 year	Species richness sig. higher in wildflower strips than in wheat fields No increase in species numbers with increasing age of strips Individual numbers sig. higher in 2-4-year-old wildflower strips than in wheat fields Increase in abundance between years 1 and 2, but then no further increase	Habitat type (A, D, C) Age (A, C) Plant species richness (C) Vegetation structure (C)		Frank & Künzle (2006)

Table 2. (Continued)

Country	Taxon	Type of strip establishment*	Habitats investigated	Sampling methods	Results	Factors influencing abundance (A), species richness (R), diversity (D), and community composition (C)	Abundant/rare species	Reference
Switzerland	Lepidoptera, Carabidae§	AES	Sown wildflower strips (n = 7–10 across different years and species groups) Conventional grasslands, ley (n = 6–11) Wheat fields (n = 6–7)	Butterfly observation Pitfall trapping of beetles Butterflies, 3 years Beetles, 2 years	Butterfly and carabid species richness sig. higher in wildflower strips than in other habitats Mean abundance of butterflies sig. higher in wildflower strips than in other habitats Mean activity density for carabids highest in wheat fields (but not sig. higher than in wildflower strips) Plant species richness explained a significant part of variation in the composition of both taxa Butterfly species richness negatively related to the percentage of crop cover	Habitat type (A, activity density) Plant species richness (C) Surrounding landscape structure (A) Year (A/activity density, R)		Aviron et al. (2007a)
Switzerland	Orthoptera, Lepidoptera, epigeal Arthropoda including Coleoptera	EP	Sown wildflower strips, without grass species (n = 8) Sown wildflower strips incl. grass species ('improved field margins') (n = 8) Conventional field margins (n = 8)	Observation of butterflies and grasshoppers Pitfall trapping of epigeal arthropods 2 years	Strips with grass and forbs mix contained sig. more butterfly and grasshopper species and individuals than wildflower strips (without sown grasses) or conventional fields Wildflower strips without grasses contained higher beetle diversity and activity density than other habitats	Habitat type (A/activity density, D) Seed mixture (A, D) Age (R)		Jacot et al. (2007)
UK	Coleoptera	EP	Countryside Stewardship mix, 7 species, grasses only Fine grass and forbs mix, 22 species Tussock grass and forbs mix, 18 species 5 replicate blocks with 9 plots (3 of each type)	Suction sampling of beetles (June and September) 1 year	Beetle abundance and species richness higher in strips with tussock grasses than with fine grasses (both incl. wildflowers) Strips with grass only did not differ in beetle abundance and diversity from the tussock-wildflower mix Percentage cover of bare ground negatively influenced abundance and species richness	Seed mixture (A, D, C) Bare ground cover (A, D) Sampling period (C) Vegetation structure (C)	All types of margins included rare species	Woodcock et al. (2005)
UK	Coleoptera	EP	As in Woodcock et al., 2005, but additionally applying three different management regimes (cutting, graminicide application, scarification)	Suction sampling of beetles 4 years	Density and species richness of predatory beetles greatest in strips including tussock grasses Phytophagous densities greatest in strips with forbs Phytophagous beetle species richness highest in strips without forbs Predatory beetle species richness highest in plots with scarification	Seed mixture (A, R, C) Management (R) Year (A, R)		Woodcock et al. (2008)

Table 2. (Continued)

Country	Taxon	Type of strip establishment*	Habitats investigated	Sampling methods	Results	Factors influencing abundance (A), species richness (R), diversity (D), and community composition (C)	Abundant/rare species	Reference
UK	Soil macrofauna including Coleoptera	EP	Winter wheat field Countryside Stewardship mix, grass species only Tussock grass and forbs mix Fine grass and forbs mix Four replicate blocks with nine plots (three of each type) and application of different management regimes	Five soil samples taken in each of the 36 plots, and 20 taken from winter wheat fields, extraction of macrofauna 1 year	Beetle abundance and diversity significantly higher in sown plots than in fields No effect of seed mixture or management on Coleoptera abundance or density in the sown plots	Habitat type (A, D) Management (C)	Most species common, one beetle species of conservation value (no preference among margin types)	Smith et al. (2008)
UK	Lepidoptera	EP	Strips sown with grasses and forbs, 23 species (n = x) Unown strips with natural regeneration (n = x) (Different management regimes were applied to both types of strips)	Butterfly observation along transects 3 years	Sown strips attracted sig. more individuals and species than unown strips Unown strips had sig. higher numbers of individuals and species than cut or sprayed strips	Habitat type (A, R) Management (A, R) Year (R)		Feber et al. (1996)
UK	Lepidoptera	AES	Strips sown with grasses, 6-9 species (n = 5) Strips with natural regeneration (n = 3) Arable field edges (n = 2)	Butterfly observation along transects 4 years	Butterfly abundance sig. higher in sown margins than in controls Strips with natural regeneration had lowest species numbers	Habitat type (A, R) Adjacent-land use (A)	Common species	Field et al. (2005)
UK	Lepidoptera	AES	Strips sown with grasses (n = 13) Arable field edges (n = 2)	Butterfly observation along transects 4 years	Butterfly abundance greater in grass margins than in controls	Habitat type (A)		Field et al. (2007)
UK	Bombidae Apis mellifera	EP	Legumes and grasses (n = 24, three different size classes) Controls, representing typical non-crop vegetation of sites (n = 8)	Bumblebee observation 1 year	Bumblebee density sig. higher in sown plots than in controls Bumblebee density did not differ sig. between plots of different size Higher abundance on patches with greater proportion of arable in surrounding landscape	Habitat type (A) Flower abundance (A) Surrounding landscape (A)		Heard et al. (2007)

Table 2. (Continued)

Country	Taxon	Type of strip establishment*	Habitats investigated	Sampling methods	Results	Factors influencing abundance (A), species richness (R), diversity (D), and community composition (C)	Abundant/rare species	Reference
UK	Bombidae	AES	Natural regeneration (n = x) Strips sown with tussock grass mixture, five species (n = x) Strips sown with grass and wildflowers, 26 species (n = x) Strips with split treatment: half tussock grasses, half grass and wildflower mixture (n = x) Cropped field edges (n = x)	Bumblebee observation along transects 3 years	Sig. higher bumblebee abundances in wildflower and split strips than all other strips/field edges in one year In another year natural regeneration had sig. higher abundances compared to tussock strips and crop edges	Habitat type (A) Seed mixture (A) Flower abundance (A) Year (A)	All six recorded bumblebee species were fairly widespread in the UK	Carvell et al. (2004)
UK	Bombidae	AES	Conventional cereal field margins (n = 58) Conservation headlands (n = 16) Strips with natural regeneration (n = 18) Strips sown with 'wildlife seed mixture' (n = 28)	Bumblebee observation along transects, paired approach of conventional field margin with one of the other margin types 1 year	Greatest abundance and species richness of bumblebees in strips with wildlife seed mixture (sig. higher than cereal field margin and conserv. headland)	Habitat type (A, R)	Most species widespread, but at least one scarce (recorded on one transect, habitat not specified)	Pywell et al. (2005)
UK	Bombidae	AES	Conventionally managed cereal crop (n = 32) Strips sown with grasses, 1-2 years old (n = 32) Strips sown with grasses, 4-11 years old (n = 32) Strips sown with grasses and wildflowers (n = 23) Strips sown with pollen- and nectar-rich species (n = 32)	Bumblebee observation along transects 1 year	A bundance sig. greater in pollen and nectar margins compared to wildflower margins (next highest abundances) and grass margins Species richness sig. greater in margins sown with either wildflowers or the pollen-nectar mix	Habitat type (A, R) Seed mixture (A, R) Flower abundance and flower richness (R) Landscape heterogeneity and % grassland (R)	Included rare species, of which 85% were found in the pollen- and nectar-rich strips	Pywell et al. (2006)
UK	Bombidae	AES	Crop (n = x) Conservation headlands (n = x) Natural regeneration (n = x) Strips sown with tussock grasses (n = x) Strips sown with wildflowers (n = x) Strips sown with pollen- and nectar-rich plants (n = x)	Bumblebee observation along transects 3 years	A bundance and species richness highest in pollen-nectar strips (sig. higher than natural regeneration or grass strips) Wildflower strips had sig. higher abundances and diversity than crop and conservation headlands all years A bundance and richness decreased over time in natural regeneration, but increased in wildflower strips	Habitat type (A, R) Seed mixture (A, R) Age (A, R) Number of bee forage flowers (A) Year (A, R)	Included rare species, mostly on pollen and nectar mix	Carvell et al. (2007)

Table 2. (Continued)

Country	Taxon	Type of strip establishment*	Habitats investigated	Sampling methods	Results	Factors influencing abundance (A), species richness (R), diversity (D), and community composition (C)	Abundant/rare species	Reference
UK	Syrphidae	EP	Wildflower patches, eight species: four grasses, four herbaceous perennials (n = 5 patches and four groups with nine smaller patches), within barley field Crop margin along disused railway line (n = 1)	Recording of aphidophagous syrphids along transects 2 years Trapping using yellow sticky traps 1 year	Field margin supported a greater diversity and density than the within-crop wildflower patches, despite a lower flower head density Patches with higher number of flowers had significantly greater aggregations of hoverflies Patch size and shape had little effect on syrphid distribution Noticeable contrast in species composition between two sampling methods	Habitat type (D, A) Flower abundance (A) Year (A)	Sutherland et al. (2001)	
UK	Aphid predators (incl Coleoptera, Diptera, Heteroptera and Neuroptera)	AES (?)	Fields with sown wildflower strips (n = 4) Fields without sown wildflower strips (n = 4)	Sticky traps along transects 1 year	Total numbers of aphid predators flying over the field sig. greater in fields with wildflower strips present, but only early in the season (May)	Presence of wildflower strip (A)	Oaten et al. (2007)	
UK	Orthoptera	AES	Strips sown with grasses, 6 m wide (n = 3) Strips sown with grasses and flowers, 6 m (n = 3) Grass tracks, 6 m (n = 3) Strips sown with flowers, 20 m (n = 3) Strips sown with grasses and flowers, 2 m (n = 3)	Standardised sweep netting 1 year	Highest abundance and species richness in strips sown with grasses and flowers	Habitat type (A, D) Seed mixture (A, D)	Marshall (2007)	
UK	Arthropoda	EP	Crop (n = 6) Strips sown with rye grass (n = 6) Strips sown with wildflowers and grasses (n = 6) Natural regeneration (n = 6)	Pitfall trapping of carabid beetles Suction sampling of arthropods Pitfall, 4 years Suction, 1 year Sampling in margins, adjacent habitat and crop (0.5 and 10 m to margin)	Highest numbers of carabids at 0.5 m distance from sown margin No difference in species numbers between different margin types Arthropod numbers highest in wildflower strips, but only sig. higher than crop (detailed results for 27 arthropod taxa are given)	Habitat type (A) Distance to margin (A) Year (A, R)	Thomas & Marshall (1999)	

Table 2. (Continued)

Country	Taxon	Type of strip establishment*	Habitats investigated	Sampling methods	Results	Factors influencing abundance (A), species richness (R), diversity (D), and community composition (C)	Abundant/rare species	Reference
UK	Apidae, Orthoptera, Carabidae**	AES	Crop edge (n = 21) Sown margin, 6 m, mostly grass species (n = 21); Paired approach	Sweep netting of bees along transects Pitfall trapping of arthropods Sweep netting and observation of grasshoppers Sampling between field edge and margin and in field centre 1 year	Sig. higher abundance and species richness of bees and Orthoptera adjacent to sown margins compared with controls or field centre Carabid numbers highest in centre of fields, no effect of sown margins on abundance Orthoptera sig. more abundant in landscapes with small fields than in open landscapes with large mean field size	Habitat type (A, R) Distance from margin (A) Landscape structure (A)		Marshall et al. (2006)
UK	Carabidae, Lepidoptera, Bombidae††	AES	Cropped field edge Strips sown with tussock grass mixture Strips sown with grasses and wildflowers Split treatment: half tussock grasses, half grass and wildflower mixture Natural regeneration	Pitfall trapping of epigeal invertebrates Observation of butterflies and bumblebees along transects 1 year	Highest abundance of butterflies and bumblebees in strips including wildflowers No sig. difference in butterfly species richness between strips Highest abundance of carabid beetles in wildflower and grass strip (but not sig. different from other strip types), lowest in crop	Habitat type (A) Seed mixture (A)	Most species common, but also less common species found (several strip types)	Meek et al. (2002)
UK	Bombidae, Lepidoptera, Coleoptera, Heteroptera	AES	Crop edge (n = 6) Conservation headland (n = 6) Natural regeneration (n = 6) Strips sown with tussock grass, five species (n = 6) Strips sown with wildflowers and grasses, 25 species incl. five grass species (n = 6) Strips sown with four legumes and four grass species (pollen and nectar mix) (n = 6)	Bumblebee and butterfly observation along transects Pitfall trapping of epigeal insects Vacuum sampling of insects 4 years	Bumblebee and butterfly abundance and species richness highest in pollen and nectar mix, followed by wildflower margins Increase in bee abundance in wildflower strips after 1 year and of butterflies after 2–3 years, decrease of bumblebees in pollen-nectar mix after 1 year and of ground-dwelling beetles in all treatments after 1 year Abundance and species richness of beetles highest in crop, conservation headland and natural regeneration in pitfall traps, but highest in pollen and nectar mix in vacuum samples Bug abundance highest in tussock strips, followed by wildflower and pollen-nectar strips	Habitat type (A, R) Seed mixture (A, R) Age (A) Year (A)		Pywell et al. (2007)
UK	Hymenoptera, Diptera (Syrphidae), Lepidoptera	EP	Wildflower patches, 12 species, no grasses (n = 2) Wildflower patches, 5 species, no grasses (n = 2) Both mixtures were sown at two different dates	Insect observation along transects 1 year	April-sown 12 species mixture had highest abundance of bees June-sown 5 species mixture had highest abundance of syrphids Phacelia attracted 87–99% of all bees Phacelia and Fagopyrum attracted most syrphids	Habitat type (A) Sowing date (A)	Both common and less common species	Carreck & Williams (1997)

Table 2. (Continued)

Country	Taxon	Type of strip establishment*	Habitats investigated	Sampling methods	Results	Factors influencing abundance (A), species richness (R), diversity (D), and community composition (C)	Abundant/rare species	Reference
UK	Hymenoptera, Diptera, Lepidoptera	EP	Wildflower patches, six species, no grasses Total of eight patches differing in sowing date, proportions and year	Insect observation along transects 2 years	Seasonal abundance of syrphids and bees differed between sowing dates Orders of insects preferred different plant species	Sowing date (A) Plant species (A)	Both common and less common species	Carreck & Williams (2002)

*EP, strips sown as experimental plots; AES, strips sown within agri-environmental scheme.

†Study includes the insect taxa Coleoptera, Diptera, Heteroptera, Homoptera, Hymenoptera, and Lepidoptera.

‡Including the insect taxa Carabidae, Staphylinidae and Coccinellidae.

§Study also includes spiders.

*n = x means that the number of replicates was not clear to us beyond all doubt.

**Study also includes spiders and birds.

††Study also includes other invertebrate groups.

wildflower patches situated within the field. Pywell *et al.* (2007) trapped higher abundances and diversity of ground dwelling beetles in crop compared with wildflower strips.

Most studies found higher abundances of investigated species groups in wildflower strips compared with sown grass margins without flowers (8 out of 13 comparisons; marginally significant). There are, however, exceptions for groups such as ground dwelling beetles and bugs, with higher abundances in grass margins than wildflower strips (Pywell *et al.*, 2007), and in other cases no differences were found (Woodcock *et al.*, 2005; beetles; Smith *et al.*, 2008; soil fauna). Regarding the species diversity of studied groups, only two studies show higher diversity in wildflower strips compared with sown grass margins (Marshall, 2007; Pywell *et al.*, 2007) while four report no difference.

Of the nine comparisons between sown wildflower strips and natural regeneration strips, six found higher abundances in the wildflower strips (Table 4, non-significant). In some cases, this is not true for all studied years or all groups, and results were not always significantly different between the two strip types. One of the two studies that found higher abundances in natural regeneration showed that abundances in wildflower strips increased over time, while they decreased in natural regeneration (Carvell *et al.*, 2007). Higher diversity in wildflower strips than natural regeneration strips was shown in three studies out of five (Feber *et al.*, 1996; Meek *et al.*, 2002; Pywell *et al.*, 2005), but also here the individual results were not always significant.

Four comparisons were made between strips with pollen- and nectar-rich plants and those with a standard wildflower mix (Pywell *et al.*, 2006, 2007; Carvell *et al.*, 2007). Although not significant because of the small number of studies, three out of four report higher abundances in the pollen-nectar mix and two out of three cases also report higher diversities there. One study noted a decline of bumblebees in the pollen and nectar mix after 1 year and an increase in the wildflower strips after 2–3 years (Pywell *et al.*, 2007).

Comparisons with grasslands are rare, but the abundance and diversity of insects in wildflower strips can be similar to that in extensive grasslands (Pfiffner & Luka, 2000; Zurbrügg & Frank, 2006) and higher than in conventional grasslands (Aviron *et al.*, 2007a).

Main pollinators: bumblebees, bees and hoverflies

Pollinators not only ensure crop pollination, but also the pollination of wild plants. Thus, decreasing numbers of pollinators can both adversely affect crop production and threaten wild plant populations (Carreck & Williams, 1997; Aizen *et al.*, 2009). The importance of restoring habitats for pollinators in intensively farmed landscapes has therefore often been highlighted (e.g. Carvell *et al.*, 2006b, 2007; Lye *et al.*, 2009; but see Ghazoul, 2005), and pollinators are mentioned as a target group for AES that include sown wildflower strips. Most studies that deal with pollinator diversity and conservation in field margins focus on bumblebees, bees and hoverflies. In general they show that areas sown with a pollen- and nectar-rich mixture attract the highest number of bumblebees and honey bees (Pywell *et al.*, 2006; Carvell *et al.*, 2007), but to support overall biodiversity

Table 3. Habitats compared in studies of wildflower strips and areas.

Compared habitats	Number of studies
SW + crop*	5
SW + margin†	6
SW + margin + crop	8
SW + grassland	1
SW + crop + grassland	2

SW, sown wildflower strip or area.

*Includes both crop and crop edge.

†Includes different types of margins or sometimes patches (pollen & nectar mixture, sown grass margins, natural regeneration).

and because of their longer flowering period, wildflower strips are also beneficial. Lye *et al.* (2009) underline the importance of considering the provision of both nectar sources and nesting sites for bumblebees.

Carreck and Williams (1997) compared pollinator diversity (of bees, bumblebees, hoverflies and butterflies) in plots in the UK sown with two different seed mixtures attractive for pollinators (Tübinger mixture from Germany with 12 species and Ascot Linde SN from the Netherlands with five species). *Phacelia* (*Phacelia tanacetifolia*) received 87–99% of bee visits, while hoverfly visits could also be observed in high numbers on buckwheat (*Fagopyrum esculentum*; Polygonales: Polygonaceae), radish (*Raphanus sativus*; Capparales: Brassicaceae) and white mustard (*Sinapis alba*; Capparales: Brassicaceae). The benefits of sowing species other than *Phacelia* were seen as low relative to the costs. In a second experiment, Carreck and Williams (2002) tested a seed mixture of six species: *phacelia* (*P. tanacetifolia*); borage (*Borago officinalis*; Lamiales: Boraginaceae), buckwheat (*F. esculentum*), cornflower (*Centaurea cyanus*; Asterales: Asteraceae), mallow (*Malva sylvestris*; Malvales: Malvaceae), and marigold (*Calendula officinalis*; Asterales: Asteraceae). This mixture attracted a large number of bees and bumblebees, as well as syrphids and some butterflies. Different insect groups preferred different plant species: *Phacelia* and *Borago* attracted most bees and bumblebees, while certain syrphid species were only observed on *Calendula* (although others were seen on *Phacelia* and *Borago*). This seed mixture is both beneficial to pollina-

tors and easy to establish, and by sowing in sequences from early spring to summer it provides a long flowering period.

More recent studies in the UK have focused on the comparison of different types of field margins (Carvell *et al.*, 2004, 2007; Pywell *et al.*, 2006). Carvell *et al.* (2004) studied bumblebee diversity and abundance in five different margin types over 3 years (margins cropped to the edge, sown with tussock grass, sown with grass and wildflowers, sown with 50% tussock grass 50% grass and wildflower mix, and natural regeneration). There were pronounced differences in the years following establishment. In the first and third year after establishment, bumblebee numbers were highest in the treatments containing wildflowers, whereas in the second year abundances were highest in the natural regeneration margins, because thistles (*Cirsium vulgare* and *C. arvense*; Asterales: Asteraceae) grew in larger numbers on two plots and attracted many bumblebees. As a result there was large variation in the pattern of flower visits between years, with over 90% of visits in the first year to *C. cyanus*, almost 60% in the second year to *Cirsium* spp., and most to birdsfoot trefoil (*Lotus corniculatus*; Fabales: Fabaceae) in the last year. Abundances were therefore to a large extent explained by the temporal availability of food resources.

A similar study of bumblebee diversity was carried out by Pywell *et al.* (2005), comparing four margin types (conventional cereal field margin, conservation headland, natural regeneration margin and sown wildflower strips) in two areas (East Anglia and West Midlands). Common species dominated the observations. The highest abundances and species richness were recorded in the sown wildflower strips, while natural regeneration margins also contained high numbers of bumblebees but fewer species. As in the study by Carvell *et al.* (2004), the main sources of attraction for bumblebees were weeds such as *Cirsium* spp. The establishment of sown wildflower strips appears to allow management of succession and therefore a way to target plants that benefit bumblebees.

In two later studies, margins sown with plants rich in pollen and nectar (a mixture of agricultural legumes) were also included (Pywell *et al.*, 2006; Carvell *et al.*, 2007). Both found that these sown strips attracted the highest abundance and diversity of bumblebees, and even rare species such as *Bombus ruderatus* and *Bombus muscorum* (Hymenoptera: Apidae) were observed (Carvell *et al.*, 2007). The pollen and nectar mixture quickly pro-

Table 4. Results of studies that compared abundances and/or diversity of insects in wildflower strips and other habitats.

	Crop, crop edge		Sown grass margins		Natural regeneration		Pollen nectar mix	
	Abundance	Diversity	Abundance	Diversity	Abundance	Diversity	Abundance	Diversity
Higher in sown wildflower strips/areas compared to other habitat	14	11	8	2	6	3	1	0
Lower in sown wildflower strips/areas compared to other habitat	2	2	2	0	2	1	3	2
No difference	0	0	3	4	1	1	0	1
<i>P</i> sign	< 0.001	0.003	0.057	0.219	0.109	0.219	0.625	0.625

One study can be represented both in different rows and columns when several habitat types were compared and when different results were obtained for different taxa. The table represents reported tendencies, not all individual differences between habitat types were significant. *P*-values are from two-tailed binomial sign tests on the results in each column.

vided very attractive foraging resources, but their combination with more traditional wildflower strips is beneficial because the latter provide resources earlier in the year and are favoured by certain bumblebee species (Carvell *et al.*, 2007). Pywell *et al.* (2006) recorded bumblebees in margins in 32 sample squares (10 × 10 km) spread over the whole of England. A comparatively high number of species were observed (nine *Bombus* species and five *Psithyrus*). Abundances were by far the greatest in the pollen and nectar mix, lower in the sown wildflower strips and very low in the other margin types. Species richness, though, was equally high in the pollen–nectar mix and the wildflower strips.

Kohler *et al.* (2008) tested the effect of flower-rich patches (10 × 10 m) on different pollinator groups (bumblebees, bees, hoverflies) in the Netherlands. These patches significantly enhanced the species density and abundance of bees and hoverflies compared with control plots. Effects on the surrounding areas were also investigated: hoverfly numbers remained elevated at distances of up to 50 m, while the numbers of bees dropped almost immediately at the boundaries of the patches.

Pest control

Aside from ensuring pollination services, a major goal of the establishment of wildflower strips is to benefit the control of agricultural pests by supporting predator species (early work reviewed by Gurr *et al.*, 2000). Several studies have investigated the abundance predators of pests within and near wildflower strips. Often there is little difference between wildflower strips and other margin types because these species are typically less dependent on floral resources, but the age of the margin and the time of year affect abundance. Pfiffner and Wyss (2004) summarised a large number of studies that show an increased number and diversity of predators in sown wildflower strips, but there is a need to more directly consider the effect of the predators on pest populations and agricultural yield.

Buchi (2002) studied the mortality of larvae of the pollen beetle *Meligethes* sp. (Coleoptera: Nitidulidae), a common pest in oilseed rape, in fields adjacent to either sown wildflower strips or meadows. Total mortality of larvae was high (66–96% depending on the year of study), but parasitism caused only 1–2% mortality and predation only 16–27%, leaving 46–72% unexplained. Larvae in fields adjacent to sown wildflower strips showed a slightly higher rate of mortality due to predation compared with fields next to meadows.

Denys and Tscharrntke (2002) compared different field margins and fallows on two experimental farms in Germany. The types of margins included natural succession (1 and 6 years old), a mixture dominated by phacelia, wildflower strips sown with 19 plant species and controls sown with cereals. The arthropod communities colonising potted plants of mugwort (*Artemisia vulgaris*; Asterales: Asteraceae) and red clover (*Trifolium pratense*; Fabales: Fabaceae) were compared in the different margins and fallows. No differences in arthropod species richness among field margins and between field margins and fallows could be found on the two potted plants. Nevertheless, there

were large differences in predator–prey ratios, with much higher ratios in the 6-year-old margins compared with others.

Studies by Oaten *et al.* (2007) and Sutherland *et al.* (2001) monitored the abundances of predators of aphids in the UK. Oaten *et al.* (2007) studied aphid predators that are known to be dispersed by air, trapping Coleoptera, Diptera, Heteroptera, and Neuroptera 1 m above the crop within fields with and without wildflower strip borders. Only early in the season (May) were aphid predators more abundant in fields with wildflower strips than without. The rest of the season there were no significant differences regarding total predator numbers, but certain groups such as Cantharidae (Coleoptera) and *Tachyporus* spp. (Coleoptera: Staphylinidae) were more abundant in fields with wildflower strips later in the season (June). The presence of aphid predators is most beneficial in spring when aphid numbers are increasing.

Sutherland *et al.* (2001) compared unsown field margins and wildflower areas of different shape within a winter barley field. They found that field margins had a higher diversity and density of aphidophagous hoverflies (Diptera: Syrphidae) than the wildflower patches, even though they contained much fewer flower heads. Among the most common species some showed a distinct affinity to the field margins (*Episyrphus balteatus*), while others did not (*Sphaerophoria* spp.). There was no difference in syrphid numbers between single large wildflower patches and groups of small patches of the same total area. Interestingly, the authors found great differences in the results between survey methods (by sight and using yellow traps), as traps are more attractive to some syrphid species than to others.

Remarkably given their potential role as biocontrol agents against crop pests, we know of no studies of the diversity and abundance of parasitoids with respect to the presence of wildflower strips.

Effects on species groups

Beetles. Coleopterans are one of the most studied insect taxa in wildflower strips. In many cases, sown wildflower strips show a greater diversity of beetles than other field margin types or habitats (Pfiffner *et al.*, 2000; Kromp *et al.*, 2004; Luka *et al.*, 2006; Aviron *et al.*, 2007a), but some studies have found that beetle abundances are not necessarily highest in the flower-rich strips, and that abundance is more dependent on factors such as vegetation structure (e.g. Woodcock *et al.*, 2005). Management can also influence beetle community composition, but field margin type is the overriding factor (Woodcock *et al.*, 2008).

Woodcock *et al.* (2005, 2007, 2008) carried out a series of studies on beetle diversity and abundance in three different field margin types in the UK. In the first year after establishment there were no differences in beetle communities between strips with grass only and those with a tussock and forbs mixture. Both margin types, however, differed from strips with fine grasses and forbs, which had the lowest abundances and species numbers. Thus, adding flower resources did not increase species diversity, suggesting that vegetation structure is more important. The beetles observed were predominantly omnivorous or predatory. No rare species were found during the study, but all margin types

included species of conservation value. To benefit overall biodiversity, the establishment of margins of different types including forbs would encourage a diverse phytophagous beetle fauna. In the following year, three different management regimes were initiated (cutting, application of graminicide and scarification of 60% of the soil surface) (Woodcock *et al.*, 2008). In this 4 year experiment, the seed mixture was identified as the most important factor explaining the structure of the beetle assemblage, while management differences resulted in further differentiation of the communities. Only scarification had a positive effect on species numbers. In a further study, seven treatments were compared varying in nutrient application, cutting regimes and aftermath grazing, all on unsown improved grasslands along field boundaries (Woodcock *et al.*, 2007). The different treatments represented different degrees of vegetation structure complexity. Treatments with minimal management (no fertilising, no grazing, few cuttings) had the highest beetle abundances and highest species numbers.

Studies from Austria and Switzerland show higher species numbers and abundances of beetles in wildflower strips compared with other field margin types or grasslands. Kromp *et al.* (2004) investigated the carabid beetle fauna in three different habitat types (sown wildflower areas, fallow with spontaneous vegetation, and arable) in the agricultural landscape of the outskirts of Vienna. To enhance biodiversity in these areas, programmes to reduce intensification have been implemented since around 2000. They found that carabid beetle numbers were highest in the sown wildflower strips, and lowest in the arable fields. Pfiffner *et al.* (2000) compared different ecological compensation areas in Switzerland and found that sown wildflower strips contributed to a diverse carabid fauna in arable land. Several species occurred only in sown wildflower strips, with xero-thermophile species and omnivores benefiting in particular. Aviron *et al.* (2007a) found that carabid species numbers were higher in wildflower strips than in conventional grasslands or wheat fields.

Comparing three different margin types in Switzerland (road verge, improved field margins and sown wildflower strips), Luka *et al.* (2006) observed that the sown wildflower strips (flower seeds only) had the highest abundances of carabid beetles and typically also the highest species richness. Nevertheless, 'improved field margins' (sown with grasses and wildflowers) offer a habitat for different species and provide an important addition to existing management schemes.

A few studies dealt in particular with the soil macrofauna, which includes many beetle species in the Carabidae and Staphylinidae. Smith *et al.* (2008) found that sown margins in the UK (with grass only or both grass and forbs) contained more beetle species in soil samples and on average twice as many individuals as the cropped areas. No significant differences in the Coleoptera fauna could be found between margins sown with different seed mixtures. Comparing different management options, scarification affected species composition but did not increase biodiversity; species assemblages in these plots were more similar to cropped fields.

Frank and Reichhart (2004) compared species richness and abundances of overwintering staphylinid (46 species) and carabid (20 species) beetles in soil samples from arable and wild-

flower strips in Switzerland. Species numbers in 1-year-old wildflower strips and arable fields did not differ, but older wildflower strips had significantly more overwintering species and individuals. The importance of wildflower strips and other semi-natural habitats as overwintering habitat for arthropods was also pointed out by Pfiffner and Luka (2000). The most abundant arthropod groups in the soil samples were Staphylinidae, Carabidae, spiders and chilopods. Semi-natural habitats had high abundances and species richness, with up to five times more overwintering arthropods in the soil samples than arable fields.

Butterflies. Several studies have investigated butterflies (Lepidoptera) in sown wildflower strips and grass margins. In the cases where comparisons were made between different margin types, butterfly numbers tend to be higher in sown wildflower strips (Feber *et al.*, 1996; Aviron *et al.*, 2007a; Haaland and Gyllin, 2010). Feber *et al.* (1996) studied different field margin treatments in the UK in relation to butterfly species numbers and abundances. Margins sown with a mixture of wildflower and grass seeds attracted more butterfly numbers and species than unsown margins. Management practice also affected butterflies, with margins left uncut during the summer attracting most butterflies, while cutting in spring, autumn or no cutting at all had no effect on individual or species numbers. In another study from the UK, Field *et al.* (2005, 2007) investigated 2 and 6 m wide sown grass margins at three farms in Essex over 4 years. The margins had higher numbers of butterflies (19 species) than control sites without margins (12 species). Some species increased over the period of the study (e.g. the meadow brown *Maniola jurtina* in 6 m grass margins or the gatekeeper *Pyronia tithonus* in 2 m margins, both Nymphalidae), but others decreased (e.g. the skippers *Thymelicus* and *Ochlodes* in 2 m margins, both Hesperidae). As a result, grass margins are considered as beneficial for butterflies since they provide larval food plants, but the effects would be greater if the margins also contained adult food sources in the form of wildflowers.

In Switzerland, Aviron *et al.* (2007a) sampled butterflies in 3 years between 2000 and 2006 in sown wildflower strips, conventional grasslands and wheat fields. A total of 33 butterfly species were recorded, with greatest species richness and abundance in wildflower strips. Habitat type and plant species richness explained a significant part of the variation. Jacot *et al.* (2007) found the highest butterfly species numbers and abundances in strips sown with grass and wildflower seeds compared with those sown with wildflowers only. Jeanneret *et al.* (2000), who studied butterflies and other species groups in different types of ecological compensation areas, found no differences between sown wildflower strips and other landscape elements regarding species numbers. The study was carried out in areas with a poor butterfly fauna, where 66–84% of all individuals belonged to *Pieris* spp. (small, large and green-veined whites; Pieridae) and in one area even common butterfly species like the meadow brown (*M. jurtina*) were absent.

Other taxa. Zurbrügg and Frank (2006) compared wildflower areas with extensively used meadows and pastures regarding abundance and species richness of bugs (Heteroptera) in Switzerland. Species richness was significantly higher in

wildflower areas and meadows compared with pastures. The highest number of predatory bug species and species overwintering in the egg stage were found in wildflower areas. Variation in species abundances could be explained by flower abundance, but not by plant species richness. Both meadows and wildflower areas were good measures to enhance bug diversity.

Two studies on grasshoppers (Orthoptera) found higher species numbers and abundances in sown margins that contain both grass and wildflower species compared with pure wildflower strips or conventional margins (Marshall, 2007; Jacot *et al.*, 2007). Marshall (2007) investigated five different margin types (sown grass margins, sown grass and flower margins of two different widths, mown grass tracks, and sown wildflower strips) for grasshoppers and crickets. The highest numbers of Orthoptera (species and abundances) were found in 2 m wide margins sown with grasses and flowers. They explain the result by the fact that margins with both grasses and flowers had the highest structural diversity and therefore offered a greater range of food resources and shelter. Jacot *et al.* (2007) found similar results in Switzerland. Grasshoppers were in some cases 40 times more abundant in margins sown with grass and wildflower seeds than in conventional field margins. Wildflower strips without grasses did not support grassland specialists, while sown wildflower strips including grasses benefit species found in fallows as well as grassland specialists.

Studies comparing wider arthropod communities

There are several studies that compare a number of different taxa across field margin types (e.g. Meek *et al.*, 2002; Marshall *et al.*, 2006; Pywell *et al.*, 2007). The overall findings are that certain margin types are more attractive to some species groups than to others, but that intensively managed field margins typically have the lowest abundances and species numbers. For example, Pywell *et al.* (2007) compare five different management regimes for margins (conservation headland, natural regeneration, sown grass margins, sown wildflower strips, and strips sown with pollen & nectar plants) for five different species groups (bumblebees, butterflies, beetles, bugs and spiders) over a period of 4 years. Their work shows that different margin types favour different species groups, but the control areas of intensively used arable land support the lowest numbers of individuals in all groups except ground dwelling beetles (and even this latter result might be related to biases in pitfall trapping due to the greater ease of movement for the epigeal fauna in this more open habitat; Melbourne, 1999). Bumblebees, butterflies and certain beetle groups (sampled with a vacuum sampler) were most common in pollen and nectar mixtures followed by sown wildflower strips, whereas the numbers of spiders and bugs were similarly high in the plots with natural regeneration and in the grass margins. There was considerable variation between years for all studied groups.

Meek *et al.* (2002) compared diversity in five different margin types (cropped to the edge, tussock grass, grass and wildflower, half tussock – half grass/wildflower, and natural regeneration). Preferences varied among the studied groups

(butterflies, bumblebees, beetles, bugs and other non-insect invertebrates), but margins cropped to the edge had lowest abundances. Overall, not surprisingly, nectar and pollen feeding insects were more abundant in margins with wildflowers. Most beetle species did not show a preference for margins of a particular type, besides avoiding the cropped edge. Different seed mixtures or types of management therefore encourage different invertebrate faunas, and all were an improvement over arable land. Most species observed during the study were common species, which could be due to the fact that the margins were investigated just 1 year after establishment. It is expected that more habitat specific species would colonise with increasing age of the margins.

Marshall *et al.* (2006) investigated different types of sown grass margins for bees and bumblebees, Orthoptera, Carabidae and other species groups (spiders and birds). Most margins were sown with a grass mixture only, but some also contained flowering species such as *Leucanthemum vulgare* and *Achillea millefolium* (both Asterales: Asteraceae). The abundance and diversity of bees, bumblebees and Orthoptera were increased in grass margins compared with controls (fields without margins), while Carabidae were not affected.

Thomas and Marshall (1999) emphasise the possibility that results of arthropod diversity in field margins can depend on the chosen sampling method. They compared four different types of sown plots (crop, rye grass, grass and flower mixture, or natural regeneration) together with the adjacent hedges and arable field. The analysis of carabids from pitfall sampling showed no significant differences between plot types, while the samples of arthropods from suction trapping showed highest species diversity and total numbers in the hedges and sown wildflower plots. Arthropod diversity was positively correlated with plant species diversity.

Factors influencing insect abundance, diversity or community structure in sown wildflower strips

Vegetation. With regard to the vegetation in wildflower strips and other margin types, a number of factors have been identified that influence insect abundance and diversity (Table 2). Six studies recognised flower abundance as an important factor for the species groups Apidae, Bombidae, Syrphidae and Heteroptera. Plant diversity was proven in two studies to affect species assemblages of Heteroptera (Frank & Künzle, 2006), Lepidoptera and Carabidae (Aviron *et al.*, 2007a). Thus, more studies show insect diversity to be correlated with floral abundance than with plant diversity, and for pollinators it is often a few plant species that are particularly attractive. Vegetation structure had an effect on abundance and on the species assemblage of Heteroptera (Frank & Künzle, 2006; Zurbrügg & Frank, 2006) and Coleoptera (Woodcock *et al.*, 2005). The species assemblage of overwintering Staphylinidae and Carabidae was influenced by vegetation cover (Frank & Reichhart, 2004).

The role of succession and age. Several studies were undertaken during sequential years or in strips of different ages, revealing changes in diversity and abundance over time. Espe-

cially where there is little management, vegetation structure and the flowering plant community changes with succession. Two studies from Switzerland showed the relationship between the condition of carabid beetles and the age of sown wildflower strips. Barone and Frank (2003) could demonstrate for the carabid *Poecilus cupreus* that reproductive condition (measured as the number of ripe eggs in females) increased with age since establishment. Nutritional condition (measured as weight and elytra length) of beetles was higher in 2–4-year-old wildflower areas than in 1-year-old ones. Additionally, both measures of condition were positively correlated with vegetation cover. Frank *et al.* (2007) studied the density and nutritional condition of five carabids (*P. cupreus*, *Agonum mülleri*, *Anchomenus dorsalis*, *Anisodactylus binotatus* and *Pterostichus vernalis*) in the same sites. The nutritional condition of all species increased mainly from the first to second year after establishment of the wildflower strips. The density of *A. binotatus* increased with the age of the wildflower strips, *A. mülleri* decreased, while the three others were not affected.

Age also affects the quality of overwintering habitat for beetles (Frank & Reichhart, 2004). Older wildflower strips had significant more species and greater abundances of overwintering staphylinids and carabids in soil samples than 1-year-old strips. Habitat age can also influence predator–prey ratios, which is important from the perspective of pest control. Denys and Tscharrntke (2002), for example, show much higher predator–prey ratios in 6-year-old margins compared with other margin types.

Several studies show mixed trends, with increases and decreases in abundances of different species over the years (Field *et al.*, 2005, 2007; Frank *et al.*, 2007), but others demonstrate a general increase in abundances, as in Luka *et al.* (2006) for bugs and cicadas and Jacot *et al.* (2007) for butterflies and grasshoppers. Changes in community structure in 4-year-old compared with 1-year-old wildflower strips have been noted by Frank and Künzle (2006). Total species richness and abundance of bugs did not differ between wildflower strips of different age, but the number of predatory bugs increased and communities became more dissimilar over the years. Carvell *et al.* (2004) could show that the attractiveness of certain margin types varied between years as a result of the availability of different food resources, and large variations in flower visits were observed between years for the same bumblebee species. In summary, it would appear that leaving wildflower strips in place for several years and ensuring that strips of different ages are available would provide the greatest overall benefits for biodiversity.

Landscape factors. The impact of landscape context on species diversity in sown wildflower strips is highlighted by several studies (e.g. Jeanneret *et al.*, 2000, 2003; Pywell *et al.*, 2006; Aviron *et al.*, 2007a; Heard *et al.*, 2007). Aviron *et al.* (2007a) found that butterfly species richness was negatively correlated with the percentage of the surrounding landscape (in a 200 m radius) that was devoted to crops. Butterfly abundance was positively related to the cover of both sown wildflower strips and of extensively managed grasslands. Beetle abundances, on the other hand, were only related to the cover of sown wildflower strips.

In the large-scale study of Pywell *et al.* (2006) in the UK, bumblebee diversity was positively correlated with landscape heterogeneity. Heard *et al.* (2007) focused in particular on the effect of the size of foraging patches and of the surrounding landscape characteristics on bumblebee abundances and diversity. The patches had a size of 0.25, 0.5 or 1 ha and were sown with a mixture of legumes and grasses, at eight sites across England. Bumblebee abundances were significantly higher in the sown patches than in control patches and increased in proportion to patch area. Bumblebee numbers increased with an increasing percentage of arable in a radius of 1 km around the patch, because of the resultant decline in alternative resources in the surrounding landscape. Kromp *et al.* (2004), on the other hand, found that colonisation of newly established wildflower areas by beetles seemed to be rather similar in the entire study area even though parts of the landscape were more heterogeneous than others.

Discussion

It can be concluded that sown wildflower strips support higher insect abundances and diversity than cropped habitats. A general exception is ground dwelling beetles, which prefer cropped areas (with some caveats due to the possibility of trapping biases). Insect abundance and diversity tends to be greater in wildflower strips than in sown grass margins and natural regeneration, but greater still in pollen and nectar mixes. For bumblebees and bees in particular, strips sown with plants that are rich in nectar and pollen are more attractive. In the few published contrasts, sown wildflower strips have comparable insect numbers and diversity to that in extensively used grasslands, despite the fact that they are recently established habitats (Pfiffner & Luka, 2000; Zurbrügg & Frank, 2006; Aviron *et al.*, 2007a). A number of studies indicate that it is predominantly common species that were found in sown wildflower strips (e.g. Meek *et al.*, 2002; Pywell *et al.*, 2005); this management scheme is thus not a panacea for rare and endangered species. As a whole, it can be argued that sown wildflower strips are a successful measure for insect conservation in agricultural areas, in that insect abundances and diversity can significantly be enhanced on arable land by providing additional resources or habitat. There is the question, however, of the extent to which populations within the wildflower strips are dependent on other nearby habitats as sources, as can be the case for field margins and semi-natural grasslands (Öckinger & Smith, 2007). To properly address this it would be necessary to make inventories in nearby habitats and before the establishment of wildflower strips. Nevertheless, in intensively used agricultural landscapes, wildflower strips can be the most suitable habitats for many insects. The fact that it is typically common species that profit from wildflower strips does not necessarily diminish their importance, since even these species are in decline in intensively used agricultural landscapes. Sown wildflower strips can thus fulfil an important function in preventing further losses of these species.

Schemes

An increasing number of countries offer schemes to promote sown wildflower strips or areas. The overall aim is to enhance biodiversity in intensively used agricultural areas and in particular to favour certain insect groups for their role as pollinators and predators. The design, management, extent of subsidy, and general conditions for farmers – as well as whether schemes are voluntary or obligatory – vary considerably between countries. A comparison of the details is, however, not easy because the relevant documents and regulation are either difficult to obtain or are only available in the national languages.

In principle three different approaches can be distinguished: wildflower strips sown with both flower and grass seeds, wildflower strips lacking grass species, and strips sown with flowers particularly rich in nectar or pollen. Regarding management, most countries advise the cutting of wildflower strips once late in the year, sometimes on a rotational basis. An exception is Switzerland, where the majority of wildflower strips are left unmanaged for up to 7 years. Different countries seem to have chosen different approaches, while some, such as the UK, offer a great variety of schemes. In Switzerland, unmanaged sown wildflower strips with a standard seed mixture of 26 flowering plants have been established for many years. Nevertheless, it has been realised that some groups prefer other seed mixtures and, as a consequence, a new scheme is now being introduced ('improved field margins', with 36 plant species and annual mowing). Why a certain scheme is designed in a certain way with a particular seed mixture in a specific country is not always clear. In any case, the conclusion that overall insect diversity is promoted by the combination of a variety of different schemes for sown margins needs to be taken into account (e.g. Meek *et al.*, 2002; Woodcock *et al.*, 2005; Luka *et al.*, 2006; Carvell *et al.*, 2007).

Implications for the design of wildflower strips

To enhance insect diversity in intensively used agricultural regions, it would be advisable to change in many cases from simple grass buffer strips to wildflower strips. That a rapid increase of wildflower strips in the landscape is possible is shown by the examples of Switzerland and Austria.

Several studies have demonstrated that different insect groups prefer different types of sown margins (e.g. Meek *et al.*, 2002; Pywell *et al.*, 2007). To promote overall insect diversity it therefore seems beneficial to combine at least three different types of scheme:

- 1 margins sown with wildflower mixtures only,
- 2 margins sown with grass seeds and wildflower seeds,
- 3 margins sown with pollen- and nectar-rich plants.

Regarding management, insect biodiversity tends to be greater in sown margins with low intensity management (Feber *et al.*, 1996; Woodcock *et al.*, 2007; Sheridan *et al.*, 2008). In most cases this is requested in schemes, typically in the form of one cutting in winter and no herbicide or insecticide treatment. The question remains as to whether no management at all – as is often practiced in sown wildflower strips in Switzerland – is

optimal. A disadvantage is that successional changes happen very quickly, with the invasion of grasses and weed species and a decrease in the sown wildflower species. On the other hand, a landscape containing these unmanaged strips is diverse, since strips of all ages co-occur. In addition, the complex structure of these strips provides undisturbed overwintering habitats. A good solution would probably be to recommend that farmers cut some of the wildflower strips in winter and leave others unmanaged.

Wildflower strips have been described as a flexible tool to enhance insect diversity (Thomas & Marshall, 1999), because the strips are relatively easy to establish or to remove by ploughing. Several studies have shown an increase in insect abundances (Denys & Tschardt, 2002) or in the condition of individual species (Barone & Frank, 2003; Frank *et al.*, 2007), in particular more than 1 year after establishment. This means that older wildflower strips will contribute more to insect diversity than new established strips. Schemes that offer subsidies for sown wildflower strips that are ploughed up again after only 1 or 2 years (as for example exist in Germany) are therefore not optimal. When sown wildflower strips are not managed, however, their value eventually decreases due to succession and the strips have to be ploughed and established again. Again, an optimal solution would be the establishment of a rolling program of mowing such that a mixture of strips of different ages is found in a given environment.

Several studies noted that common species were the main beneficiaries of the presence of sown margins (e.g. Meek *et al.*, 2002; Pywell *et al.*, 2005). This, together with the fact that a number of studies show an influence of landscape factors on species diversity in the wildflower strips, indicates that their success in increasing insect biodiversity has its limits. Wildflower strips can, of course, only become a habitat for species that are able to colonise them, so that dispersal ability and landscape structure interact to determine the benefit to individual species. As a result, sown wildflower strips might often represent an instrument to enhance or preserve insect species that are rather widespread and common in agricultural landscapes. Nevertheless, these species too have seen their habitat decline in intensively used areas.

That rare species can also benefit from wildflower strips is demonstrated by the case of the mallow skipper (*Carcharodus alceae*; Lepidoptera: Hesperidae). It is a threatened species in Switzerland, but due to the fact that its larval food plant (*Malva*) is part of the standard wildflower seed mix, the species has become much more abundant (Wermeille & Carron, 2005). In a similar way, the swallowtail (*Papilio machaon*; Lepidoptera: Papilionidae) uses *Pastinaca* (Apiaceae: Apiaceae) in the sown wildflower strips as a larval food plant. This shows that the success of wildflower strips can be enhanced by a careful selection of the sown species to benefit particular target species. The seed mix should also be tailored to provide resources for all life history stages, for example, larval host plants and adult nectar sources in butterflies.

An important aspect for the conservation of species, and especially of those that are less mobile, is that wildflower strips can serve as corridors to connect isolated habitats. Thus, the geographical arrangement of strips should be carefully planned.

There is, however, a lack of research testing this specific function, despite the fact that the creation of networks is often cited as a motivation for such AES.

Finally, the success of certain AES including sown wildflower strips is dependent on their acceptance and popularity (especially where schemes are voluntarily). In that perspective, sown wildflower strips seem to be appreciated by farmers and the public compared with other margin types (Marshall & Moonen, 2002). Mante and Gerowitt (2007), for example, found that farmers preferred field margins that can be sown with a particular seed mixture (both grass and wildflower mixtures) compared with margins with natural succession. Jacot *et al.* (2002, 2007) found that both farmers and the public had a positive attitude towards sown wildflower strips. It seems therefore that wildflower strips, by careful choice of seed mix and management, can successfully combine roles in human amenity, ecosystem services such as pollination and pest control, and conservation.

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References

- Aizen, M.A., Garibaldi, L.A., Cunningham, S.A. & Klein, A.M. (2009) How much does agriculture depend on pollinators? Lessons from long-term trends in crop production. *Annals of Botany*, **103**, 1579–1588.
- Albrecht, M., Duelli, P., Muller, C., Kleijn, D. & Schmid, B. (2007) The Swiss agri-environment scheme enhances pollinator diversity and plant reproductive success in nearby intensively managed farmland. *Journal of Applied Ecology*, **44**, 813–822.
- Aviron, S., Herzog, F., Klaus, I., Luka, H., Pfiffner, L., Schupbach, B. & Jeanneret, P. (2007a) Effects of Swiss agri-environmental measures on arthropod biodiversity in arable landscapes. *Aspects of Applied Biology*, **81**, 101–109.
- Backman, J.P.C. & Tiainen, J. (2002) Habitat quality of field margins in a Finnish farmland area for bumblebees (Hymenoptera: *Bombus* and *Psithyrus*). *Agriculture, Ecosystems & Environment*, **89**, 53–68.
- Barone, M. & Frank, T. (2003) Habitat age increases reproduction and nutritional condition in a generalist arthropod predator. *Oecologia*, **135**, 78–83.
- Benton, T.G., Vickery, J.A. & Wilson, J.D. (2003) Farmland biodiversity: is habitat heterogeneity the key? *Trends in Ecology & Evolution*, **18**, 182–188.
- Berendse, F., Chamberlain, D., Kleijn, D. & Schekkerman, H. (2004) Declining biodiversity in agricultural landscapes and the effectiveness of agri-environment schemes. *Ambio*, **33**, 499–502.
- Biesmeijer, J.C., Roberts, S.P.M., Reemer, M., Ohlemuller, R., Edwards, M., Peeters, T., Schaffers, A.P., Potts, S.G., Kleukers, R., Thomas, C.D., Settele, J. & Kunin, W.E. (2006) Parallel declines in pollinators and insect-pollinated plants in Britain and the Netherlands. *Science*, **313**, 351–354.
- Boatman, N.D., Davies, D.H.K., Chaney, K., Feber, R. & Sparks, T.H. (1999) *Aspects of Applied Biology 54: Field Margins and Buffer Zones: Ecology, Management and Policy*. Association of Applied Biologists, Wellesbourne, UK.
- Buchi, R. (2002) Mortality of pollen beetle (*Meligethes* spp.) larvae due to predators and parasitoids in rape fields and the effect of conservation strips. *Agriculture, Ecosystems & Environment*, **90**, 255–263.
- Carreck, N.L. & Williams, I.H. (1997) Observations on two commercial flower mixtures as food sources for beneficial insects in the UK. *Journal of Agricultural Science*, **128**, 397–403.
- Carreck, N.L. & Williams, I.H. (2002) Food for insect pollinators on farmland: insect visits to flowers of annual seed mixtures. *Journal of Insect Conservation*, **6**, 13–23.
- Carvell, C., Meek, W.R., Pywell, R.F., Goulson, D. & Nowakowski, M. (2007) Comparing the efficacy of agri-environment schemes to enhance bumble bee abundance and diversity on arable field margins. *Journal of Applied Ecology*, **44**, 29–40.
- Carvell, C., Meek, W.R., Pywell, R.F. & Nowakowski, M. (2004) The response of foraging bumblebees to successional change in newly created arable field margins. *Biological Conservation*, **118**, 327–339.
- Carvell, C., Roy, D.B., Smart, S.M., Pywell, R.F., Preston, C.D. & Goulson, D. (2006a) Declines in forage availability for bumblebees at a national scale. *Biological Conservation*, **132**, 481–489.
- Carvell, C., Westrich, P., Meek, W.R., Pywell, R.F. & Nowakowski, M. (2006b) Assessing the value of annual and perennial forage mixtures for bumblebees by direct observation and pollen analysis. *Apidologie*, **37**, 326–340.
- Conrad, K.F., Perry, J.N., Woiwod, I.P. & Alexander, C.J. (2006) Large-scale temporal changes in spatial pattern during declines of abundance and occupancy in a common moth. *Journal of Insect Conservation*, **10**, 53–64.
- Denys, C. & Tschardtke, T. (2002) Plant-insect communities and predator-prey ratios in field margin strips, adjacent crop fields, and fallows. *Oecologia*, **130**, 315–324.
- Diekötter, T., Billeter, R. & Crist, T.O. (2008) Effects of landscape connectivity on the spatial distribution of insect diversity in agricultural mosaic landscapes. *Basic and Applied Ecology*, **9**, 298–307.
- European Commission. Available from URL: http://ec.europa.eu/agriculture/rurdev/countries/index_en.htm.
- Feber, R.E., Smith, H. & Macdonald, D.W. (1996) The effects on butterfly abundance of the management of uncropped edges of arable fields. *Journal of Applied Ecology*, **33**, 1191–1205.
- Feehan, J., Gillmor, D.A. & Culleton, N. (2005) Effects of an agri-environment scheme on farmland biodiversity in Ireland. *Agriculture, Ecosystems & Environment*, **107**, 275–286.
- Field, R.G., Gardiner, T., Mason, C.F. & Hill, J. (2005) Agri-environment schemes and butterflies: the utilisation of 6 m grass margins. *Biodiversity and Conservation*, **14**, 1969–1976.
- Field, R.G., Gardiner, T., Mason, C.F. & Hill, J. (2007) Agri-environment schemes and butterflies: the utilisation of two metre arable field margins. *Biodiversity and Conservation*, **16**, 465–474.
- Finland, Ministry of Agriculture and Forestry. Available from URL: http://www.mmm.fi/en/index/frontpage/rural_areas/rural-developmentprogrammes/strategyandprogramme20072013.html.
- Fitzpatrick, U., Murray, T.E., Paxton, R.J., Breen, J., Cotton, D., Santorum, V. & Brown, M.J.F. (2007) Rarity and decline

- in bumblebees – a test of causes and correlates in the Irish fauna. *Biological Conservation*, **136**, 185–194.
- Frank, T., Kehrl, P. & Germann, C. (2007) Density and nutritional condition of carabid beetles in wildflower areas of different age. *Agriculture, Ecosystems & Environment*, **120**, 377–383.
- Frank, T. & Künzle, I. (2006) Effect of early succession in wildflower areas on bug assemblages (Insecta: Heteroptera). *European Journal of Entomology*, **103**, 61–70.
- Frank, T. & Reichhart, B. (2004) Staphylinidae and Carabidae overwintering in wheat and sown wildflower areas of different age. *Bulletin of Entomological Research*, **94**, 209–217.
- Germany, Lower Saxony & Bremen, Ministry for Food, Agriculture, Consumer Protection and Rural Development. Available from URL: http://www.ml.niedersachsen.de/master/C20359226_N20358583_L20_D0_I655.html (in German only).
- Ghazoul, J. (2005) Buzziness as usual? Questioning the global pollination crisis. *Trends in Ecology & Evolution*, **20**, 367–373.
- Goulson, D., Lye, G.C. & Darvill, B. (2008) Decline and conservation of bumble bees. *Annual Review of Entomology*, **53**, 191–208.
- Gurr, G.M., Wratten, S.D. & Barbosa, P. (2000) Success in conservation biological control of arthropods. *Biological Control: Measures of Success* (ed. by G.M. Gurr and S.D. Wratten), pp. 105–132. Kluwer Academic Publishers, Dordrecht, The Netherlands.
- Haaland, C. & Gyllin, M. (2010) Butterflies and bumblebees in greenways and sown wildflower strips in southern Sweden. *Journal of Insect Conservation*, **14**, 125–132.
- Haslett, J.R. (2007) *European Strategy for the Conservation of Invertebrates*. Council of Europe Publishing, Strasbourg, France.
- Heard, M.S., Carvell, C., Carreck, N.L., Rothery, P., Osborne, J.L. & Bourke, A.F.G. (2007) Landscape context not patch size determines bumble-bee density on flower mixtures sown for agri-environment schemes. *Biology Letters*, **3**, 638–641.
- Jacot, K., Eggenschwiler, L., Junge, X., Luka, H. & Bosshard, A. (2007) Improved field margins for a higher biodiversity in agricultural landscapes. *Aspects of Applied Biology*, **81**, 277–283.
- Jacot, K., Eggenschwiler, L. & Studer, S. (2002) Wild flower strips and rotational fallow: experiences from the practice. *Agrarforschung*, **9**, 146–151.
- Jeanneret, P., Schupbach, B., Pfiffner, L. & Walter, T. (2003) Arthropod reaction to landscape and habitat features in agricultural landscapes. *Landscape Ecology*, **18**, 253–263.
- Jeanneret, P., Schupbach, B., Steiger, J., Waldburger, M. & Bigler, F. (2000) Evaluation of ecological measures: biodiversity. Spiders and butterflies. *Agrarforschung*, **7**, 112–116.
- Jongman, R.H.G. (2002) Homogenisation and fragmentation of the European landscape: ecological consequences and solutions. *Landscape and Urban Planning*, **58**, 211–221.
- Kleijn, D., Baquero, R.A., Clough, Y., Diaz, M., De Esteban, J., Fernandez, F., Gabriel, D., Herzog, F., Holzschuh, A., Johl, R., Knop, E., Kruss, A., Marshall, E.J.P., Steffan-Dewenter, I., Tscharrntke, T., Verhulst, J., West, T.M. & Yela, J.L. (2006) Mixed biodiversity benefits of agri-environment schemes in five European countries. *Ecology Letters*, **9**, 243–254.
- Kleijn, D. & Sutherland, W.J. (2003) How effective are European agri-environment schemes in conserving and promoting biodiversity? *Journal of Applied Ecology*, **40**, 947–969.
- Kohler, F., Verhulst, J., Knop, E., Herzog, F. & Kleijn, D. (2007) Indirect effects of grassland extensification schemes on pollinators in two contrasting European countries. *Biological Conservation*, **135**, 302–307.
- Kohler, F., Verhulst, J., van Klink, R. & Kleijn, D. (2008) At what spatial scale do high-quality habitats enhance the diversity of forbs and pollinators in intensively farmed landscapes? *Journal of Applied Ecology*, **45**, 753–762.
- Kosior, A., Celary, W., Olejniczak, P., Fijał, J., Krol, W., Solarz, W. & Plonka, P. (2007) The decline of the bumble bees and cuckoo bees (Hymenoptera: Apidae: Bombini) of Western and Central Europe. *Oryx*, **41**, 79–88.
- Kotze, D.J. & O'Hara, R.B. (2003) Species decline – but why? Explanations of carabid beetle (Coleoptera, Carabidae) declines in Europe. *Oecologia*, **135**, 138–148.
- Kromp, B., Hann, P., Kraus, P. & Meindl, P. (2004) Viennese Programme of Contracted Nature Conservation 'Biotop Farmland': monitoring of carabids in sown wildflower strips and adjacent fields. *Mitteilungen der Deutschen Gesellschaft für Allgemeine und Angewandte Entomologie*, **14**, 509–512.
- Kruss, A. & Tscharrntke, T. (1994) Habitat fragmentation, species loss, and biological-control. *Science*, **264**, 1581–1584.
- Kuussaari, M., Heliola, J., Poyry, J. & Saarinen, K. (2007) Contrasting trends of butterfly species preferring semi-natural grasslands, field margins and forest edges in northern Europe. *Journal of Insect Conservation*, **11**, 351–366.
- Lips, A., Harding, J., Schüpbach, B., Jeanneret, P. & Bigler, F. (2000) Botanische Vielfalt von Wiesen in drei Fallstudiengebieten. *Agrarforschung*, **7**, 106–111.
- Luka, H., Uehlinger, G., Pfiffner, L., Muhlethaler, R. & Blick, T. (2006) Extended field margins – a new element of ecological compensation in farmed landscapes – deliver positive impacts for Articulata. *Agrarforschung*, **13**, 386–391.
- Lye, G., Park, K., Osborne, J., Holland, J. & Goulson, D. (2009) Assessing the value of Rural Stewardship schemes for providing foraging resources and nesting habitat for bumblebee queens (Hymenoptera: Apidae). *Biological Conservation*, **142**, 2023–2032.
- Maes, D. & Van Dyck, H. (2001) Butterfly diversity loss in Flanders (north Belgium): Europe's worst case scenario? *Biological Conservation*, **99**, 263–276.
- Mand, M., Mand, R. & Williams, I.H. (2002) Bumblebees in the agricultural landscape of Estonia. *Agriculture, Ecosystems & Environment*, **89**, 69–76.
- Mante, J. & Gerowitt, B. (2007) On perspectives for flowering field boundaries in intensively used agricultural regions. *Gesunde Pflanzen*, **59**, 71–76.
- Marshall, E.J.P. (2007) The effect of arable field margin structure and composition on Orthoptera assemblages. *Aspects of Applied Biology*, **81**, 231–238.
- Marshall, E.J.P. & Moonen, A.C. (2002) Field margins in northern Europe: their functions and interactions with agriculture. *Agriculture, Ecosystems & Environment*, **89**, 5–21.
- Marshall, E.J.P., West, T.M. & Kleijn, D. (2006) Impacts of an agri-environment field margin prescription on the flora and fauna of arable farmland in different landscapes. *Agriculture, Ecosystems & Environment*, **113**, 36–44.
- Meek, W.M., Loxton, D., Sparks, T.H., Pywell, R., Pickett, H. & Nowakowski, M. (2002) The effect of arable field margin composition on invertebrate biodiversity. *Biological Conservation*, **106**, 259–271.
- Melbourne, B.A. (1999) Bias in the effect of habitat structure on pitfall traps: an experimental evaluation. *Austral Ecology*, **24**, 228–239.

- Nentwig, W. (ed.) (2000) *Streifenförmige Ökologische Ausgleichsflächen in der Kulturlandschaft: Ackerkrautstreifen, Buntbrachen, Feldränder*. Verlag Agrarökologie, Bern, Switzerland/Hannover, Germany.
- Nilsson, S.G., Franzén, M. & Jönsson, E. (2008) Long-term land-use changes and extinction of specialised butterflies. *Insect Conservation and Diversity*, **1**, 197–207.
- Oaten, H., Holland, J.M. & Smith, B.M. (2007) Attack from above: the effect of field margins on movements of aerially dispersing aphid predators. *Aspects of Applied Biology*, **83**, 89–93.
- Öckinger, E. & Smith, H.G. (2007) Semi-natural grasslands as populations sources for pollinating insects in agricultural landscapes. *Journal of Applied Ecology*, **44**, 50–59.
- Pfiffner, L. & Luka, H. (2000) Overwintering of arthropods in soils of arable fields and adjacent semi-natural habitats. *Agriculture, Ecosystems & Environment*, **78**, 215–222.
- Pfiffner, L., Luka, H., Jeanneret, P. & Schupbach, B. (2000) Effects of ecological compensation areas on the carabid fauna. *Agrarforschung*, **7**, 212–217.
- Pfiffner, L. & Wyss, E. (2004) Use of sown wildflower strips to enhance natural enemies of agricultural pests. *Ecological Engineering for Pest Management: Advances in Habitat Manipulation for Arthropods* (ed. by G.M. Gurr, S.D. Wratten and M.A. Altieri), pp. 165–186. CSIRO Publishing, Collingwood, Victoria, Australia.
- Polus, E., Vandewoestijne, S., Choutt, J. & Baguette, M. (2007) Tracking the effects of one century of habitat loss and fragmentation on calcareous grassland butterfly communities. *Biodiversity and Conservation*, **16**, 3423–3436.
- Potts, S.G., Bradbury, R.B., Mortimer, S.R. & Woodcock, B.A. (2006) Commentary on Kleijn *et al.* 2006. *Ecology Letters*, **9**, 254–256.
- Pywell, R.F., Meek, W.M., Carvell, C., Hulmes, L. & Nowakowski, M. (2007) The Buzz project: biodiversity enhancement on arable land under the new agri-environment schemes. *Aspects of Applied Biology*, **81**, 61–68.
- Pywell, R.F., Warman, E.A., Carvell, C., Sparks, T.H., Dicks, L.V., Bennett, D., Wright, A., Critchley, C.N.R. & Sherwood, A. (2005) Providing foraging resources for bumblebees in intensively farmed landscapes. *Biological Conservation*, **121**, 479–494.
- Pywell, R.F., Warman, E.A., Hulmes, L., Hulmes, S., Nuttall, P., Sparks, T.H., Critchley, C.N.R. & Sherwood, A. (2006) Effectiveness of new agri-environment schemes in providing foraging resources for bumblebees in intensively farmed landscapes. *Biological Conservation*, **129**, 192–206.
- Scott, R. (1996) Creating successful and popular wildflower landscapes. *Aspects of Applied Biology*, **44**, 475–480.
- Sheridan, H., Finn, J.A., Culleton, N. & O'Donovanc, G. (2008) Plant and invertebrate diversity in grassland field margins. *Agriculture, Ecosystems & Environment*, **123**, 225–232.
- Smith, J., Potts, S.G., Woodcock, B.A. & Eggleton, P. (2008) Can arable field margins be managed to enhance their biodiversity, conservation and functional value for soil macrofauna? *Journal of Applied Ecology*, **45**, 269–278.
- Stoate, C., Boatman, N.D., Borralho, R.J., Carvalho, C.R., de Snoo, G.R. & Eden, P. (2001) Ecological impacts of arable intensification in Europe. *Journal of Environmental Management*, **63**, 337–365.
- Sutherland, J.P., Sullivan, M.S. & Poppy, G.M. (2001) Distribution and abundance of aphidophagous hoverflies (Diptera: Syrphidae) in wildflower patches and field margin habitats. *Agricultural and Forest Entomology*, **3**, 57–64.
- van Swaay, C., Warren, M. & Lois, G. (2006) Biotope use and trends of European butterflies. *Journal of Insect Conservation*, **10**, 189–209.
- Sweden, Ministry of Agriculture. Available from URL: <http://www.regeringen.se/sb/d/10158/a/82727>.
- Sweden, Swedish Board of Agriculture. Available from URL: <http://www.jordbruksverket.se/amnesomraden/stod/ersattningforutvaldmiljo/mangfaldstrada.4.6a459c18120617aa58a80001921.html>.
- Thomas, C.F.G. & Marshall, E.J.P. (1999) Arthropod abundance and diversity in differently vegetated margins of arable fields. *Agriculture, Ecosystems & Environment*, **72**, 131–144.
- Tscharntke, T., Klein, A.M., Kruess, A., Steffan-Dewenter, I. & Thies, C. (2005) Landscape perspectives on agricultural intensification and biodiversity – ecosystem service management. *Ecology Letters*, **8**, 857–874.
- UK, Department for Environment, Food and Rural Affairs. Available from URL: <http://www.defra.gov.uk/rural/rdpe/progdoc.htm>.
- Websites to 'Rural development programmes, 2007–2013'. Austria, Lebensministerium. Available from URL: <http://land.lebensministerium.at/article/articleview/60503/1/21434> (in German only).
- Wenzel, M., Schmitt, T., Weitzel, M. & Seitz, A. (2006) The severe decline of butterflies on western German calcareous grasslands during the last 30 years: a conservation problem. *Biological Conservation*, **128**, 542–552.
- Wermeille, E. & Carron, G. (2005) Value of fallows for the Mallo Skipper (*Carcharodus alceae*) and some other butterfly species. *Revue Suisse d'Agriculture*, **37**, 175–182.
- Whitfield, J. (2006) How green was my subsidy? *Nature*, **439**, 908–909.
- Whittingham, M.J. (2007) Will agri-environment schemes deliver substantial biodiversity gain, and if not why not? *Journal of Applied Ecology*, **44**, 1–5.
- Woodcock, B.A., Potts, S.G., Pilgrim, E., Ramsay, A.J., Tscheulin, T., Parkinson, A., Smith, R.E.N., Gundry, A.L., Brown, V.K. & Tallowin, J.R. (2007) The potential of grass field margin management for enhancing beetle diversity in intensive livestock farms. *Journal of Applied Ecology*, **44**, 60–69.
- Woodcock, B.A., Westbury, D.B., Potts, S.G., Harris, S.J. & Brown, V.K. (2005) Establishing field margins to promote beetle conservation in arable farms. *Agriculture, Ecosystems & Environment*, **107**, 255–266.
- Woodcock, B.A., Westbury, D.B., Tscheulin, T., Harrison-Cripps, J., Harris, S.J., Ramsey, A.J., Brown, V.K. & Potts, S.G. (2008) Effects of seed mixture and management on beetle assemblages of arable field margins. *Agriculture, Ecosystems & Environment*, **125**, 246–254.
- Zurbrugg, C. & Frank, T. (2006) Factors influencing bug diversity (Insecta: Heteroptera) in semi-natural habitats. *Biodiversity and Conservation*, **15**, 275–294.